

THE RHYNCHONELLIDE BRACHIOPOD *EOCOELIA* FROM THE UPPER LLANDOVERY OF IRELAND AND SCOTLAND

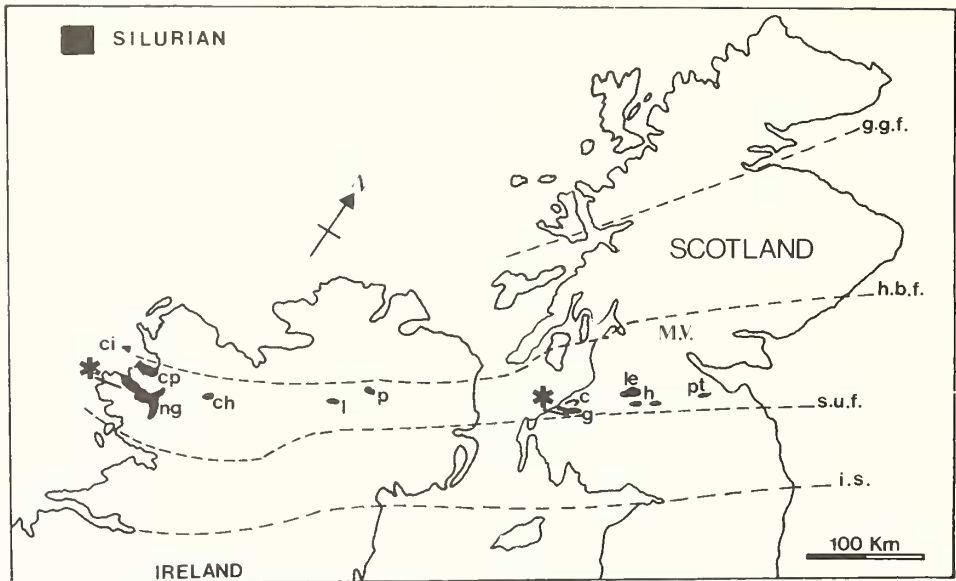
by E. N. DOYLE, A. N. HÖEY and D. A. T. HARPER

ABSTRACT. Biometrical description of large samples ($N > 300$) of the rhynchonellide brachiopod *Eocoelia* from the Kilbride Formation (upper Telychian) in the west of Ireland and the Lower Camregan Grits (lower Telychian) of the Girvan district, south-west Scotland, suggests the refinement of the stratigraphically important *Eocoelia* lineage in the upper Llandoverly. The Irish and Scottish species have previously both been assigned to *Eocoelia curtisi* Ziegler. However, the Girvan population is significantly different from type and topotype specimens from Tortworth and from the Irish material. The Scottish form is accorded separate subspecific status, *Eocoelia curtisi immatura* subsp. nov., whereas the Irish form is included in the nominate subspecies. The Irish and Scottish subspecies are within the upper and lower parts of the range of *E. curtisi* s.l. respectively. Interpolation within the lineage confirms some of the established morphological transpecific trends and may permit more precise correlation within the upper Llandoverly.

THE distinctive rhynchonellide brachiopod *Eocoelia* Nikiforova, 1961 (*in* Nikiforova and Andreeva 1961) has been of considerable importance in studies of Silurian benthos. First, the genus is the eponymous component of the widespread *Eocoelia* Community which occupied nearshore environments during the late Llandoverly (Ziegler 1965), and secondly the well-documented *Eocoelia* lineage has been effectively used in biostratigraphical correlation within lower Silurian shelly facies (Ziegler 1966). Detailed biometrical analysis of *Eocoelia* from the west of Ireland and south-west Scotland has permitted a significant refinement of the existing Llandoverly part of the *Eocoelia* lineage which has some bearing on correlation at and near the base of the Telychian. The analysis, however, confirms some problems in the application of conventional Linnean nomenclature in such gradualist lineages (e.g. Sheldon 1987).

DISTRIBUTION OF *EOCOELIA* IN IRELAND AND SCOTLAND

Eocoelia is relatively widespread throughout the lower Silurian of the Anglo-Welsh area but its distribution is comparatively more localized across Ireland and Scotland. The occurrences in the west of Ireland and Girvan are the only records of the genus from the Midland Valley of Scotland and its Irish equivalent (Text-fig. 1). Two species of *Eocoelia* have been recorded from the West of Ireland. *E. curtisi* Ziegler dominates shell beds within the lower part of the Kilbride Formation along the Silurian outcrop of North Connemara and on the Kilbride Peninsula (Piper 1972); *E. angelini* occurs in the lower Wenlock Lough Muck Formation (*E. sulcata* *in* Laird and McKerrow 1970). Large new collections of *E. curtisi* have been made from three localities within the lower part of the Kilbride Formation along the Llandoverly outcrop in north Connemara as follows: I1, Lough Fee (IGR L 609790); I2, Lettershanbally (IGR L 584836); I3, Lee (IGR L 570 885) (see also Doyle 1989). In the Girvan district, SW Scotland, *Eocoelia* has long been known from the Lower Camregan Grits of the Main Silurian Outcrop, south of the Girvan Valley, in Penwhapple Burn and adjacent areas (Davidson 1867). A. N. H. has made substantial new collections from three localities within the Lower Camregan Grits in the Penwhapple Burn area as follows: S1, (NGR NX 2271 9807); S2, (NGR NX 2230 9799); and S3, (NGR NX 2254 9805); and a new occurrence of the genus is recorded from the Craighead inlier where it occurs with *Pentameroides*.



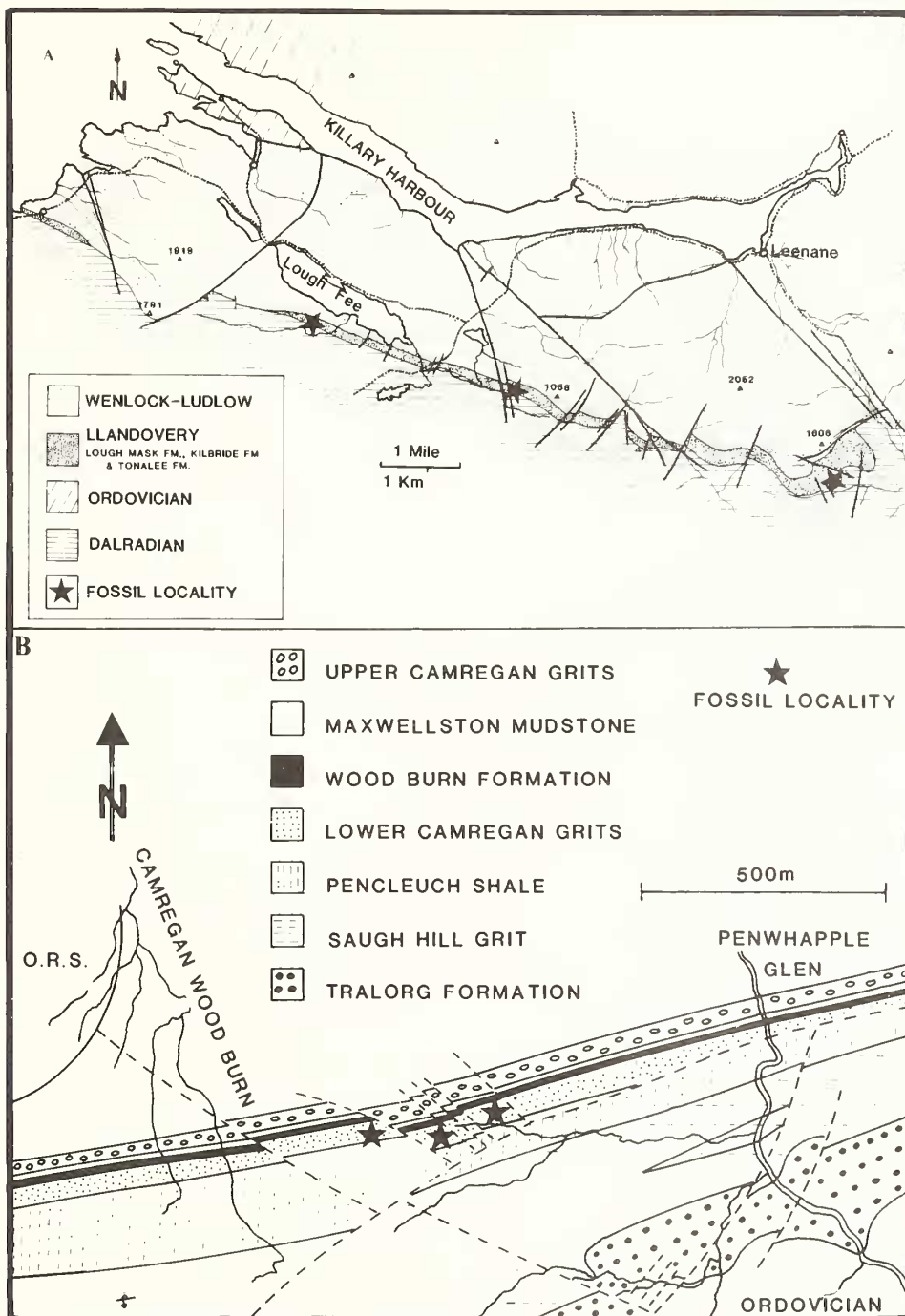
TEXT-FIG. 1. Location of upper Llandovery *Eocoelia* in the Midland Valley of Scotland and its Irish equivalent. Abbreviations: ci, Clare Island; cp, Croagh Patrick; ng, North Galway; ch, Charlestown; l, Lisbellaw; p, Pomeroy; c, Craighead inlier; g, Main Outcrop, Girvan; le, Lesmahagow; h, Hagshaw Hills; pt, Pentland Hills; g.g.f., Great Glen fault; h.b.f., Highland Boundary fault; s.u.f., Southern Upland fault; i.s., putative track of Iapetus suture; M.V., Midland Valley. Occurrence of *Eocoelia* indicated by asterisk.

MORPHOLOGICAL ANALYSIS

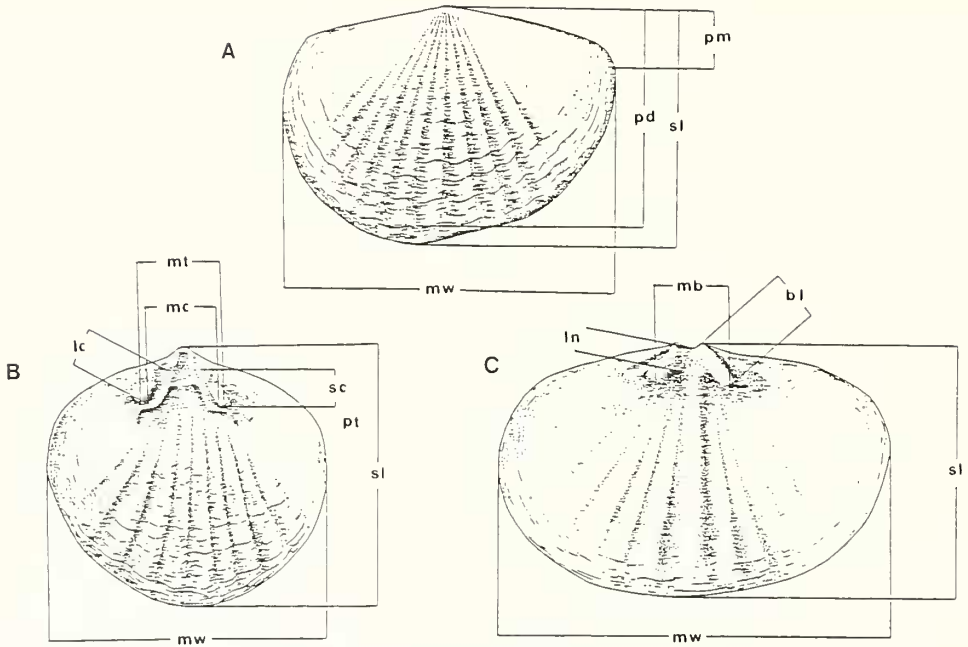
Large samples of *Eocoelia* from Girvan ($N = 342$) and Connemara ($N = 419$) together with a more limited sample of topotype material of *E. curtisi* from the Tortworth inlier were analysed with reference to a set of continuous variates defined below and illustrated on Text-figure 3A–C. The ribbing patterns of all three samples were investigated with the aid of frequency histograms and non-parametric inferential statistics. All graphical and statistical analyses were processed by the PALSTAT package (Harper and Ryan 1987) implemented on a BBC B microcomputer.

Measurements taken (in mm) were sl, sagittal length; mw, maximum width; pm, position of maximum width measured from posterior margin; pt, position of maximum depth measured from posterior margin; pd, position of deflection measured along sagittal length; nr, total number of ribs; lc, total length of crural fossettes; mc, maximum separation of crural fossettes; sc, sagittal length of crural fossettes; mt, maximum separation of teeth; mb, maximum separation of distal ends of the brachiophores; bl, maximum length of brachiophores; ln, length of notothyrial platform. Matrices of sample sizes are shown in Table 1.

Pooled samples both of the brachial and pedicle valve exteriors and interiors from Connemara, Girvan and Tortworth were investigated for size-independent variation within and between samples using the multivariate technique of Principal Component Analysis (PCA); the relationships between the continuous variates, defined above, are described by a correlation matrix from which the appropriate eigenvalues and eigenvectors have been extracted. The rib counts, defined as the total number of costae, for all three samples are displayed as frequency polygons (Text-figs 4 and 5) compared using the non-parametric Kolmogorov–Smirnov test, whilst the rib strength (height/width ratio calculated as a percentage) was similarly investigated by histograms together with parametric and non-parametric inferential statistics (Text-figs 6 and 7). Three features of shell morphology yielded taxonomically significant results: (i) size-independent shape variation between samples of valve exteriors, (ii) the total number of ribs, and (iii) the strength of ribs.



TEXT-FIG. 2. Locality details and stratigraphies for the *Eoecolia*-bearing horizons sampled in the West of Ireland (A) and Girvan, SW Scotland (B).



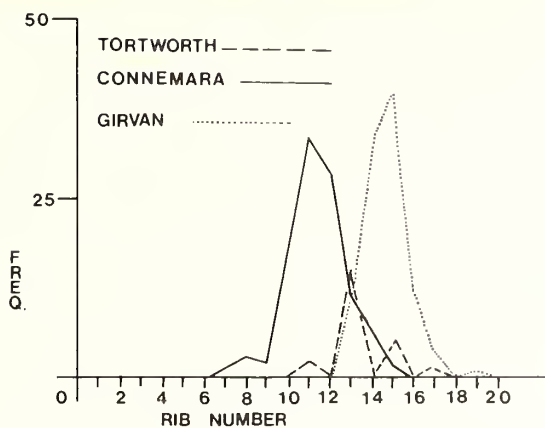
TEXT-FIG. 3. Location of measurements made on the exteriors (A) and ventral (B) and dorsal (C) interiors of *Eocoelia*. Abbreviations and definition of measurements given in text.

TABLE 1. Matrices of sample sizes. Abbreviations: PVE, pedicle valve exterior; PVI, pedicle valve interior; BVE, brachial valve exterior; BVI, brachial valve interior.

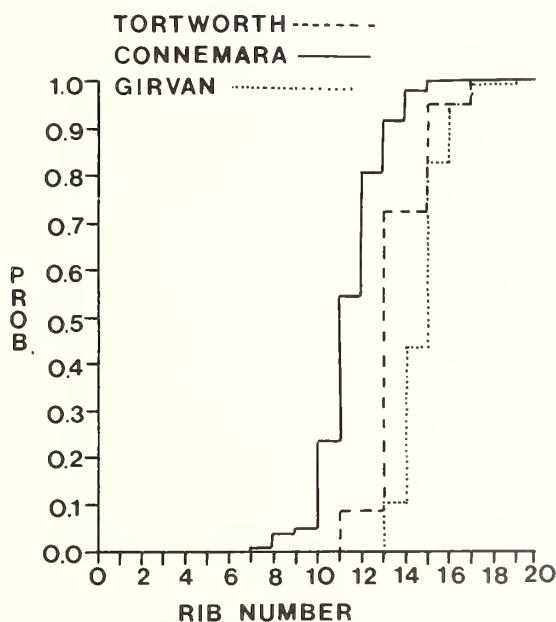
Locality	Girvan				Connemara			
	S1	S2	S3	Total	I1	I2	I3	Total
Valve								
PVE	47	37	33	117	33	35	33	101
PVI	15	11	18	44	32	32	32	96
BVE	33	35	35	102	38	40	33	111
BVI	25	19	35	79	33	45	33	111

Pooled samples of the Connemara, Girvan and Tortworth specimens were investigated by PCA: both pedicle and brachial valve exteriors and interiors were analysed with reference to the variates defined above. The investigation of comparative internal morphology, with reference to the following variates – sl, mw, mb, bl and ln for brachial valves and sl, mw, lc, mc, sc and mt for pedicle valves – yielded no apparent differences between the three samples when each specimen was plotted relative to the second and subsequent (size-independent) eigenvectors. The Irish specimens have markedly larger scores on the first eigenvector, confirming their relatively larger size. However, multivariate examination of the valve exteriors based on the variates sl, mw and pm suggests the samples may also be differentiated with reference to their scores on the second eigenvector (direction cosines: -0.278 , -0.423 and 0.862) of this analysis; the Irish specimens had significantly lower scores on this eigenvector indicating an outline with a maximum width, on average, nearer the posterior margin (Text-fig. 8).

Significant differences in the rib counts were detected between the Girvan material and the specimens from both Connemara and Tortworth (Text-fig. 5). The Tortworth sample appears to

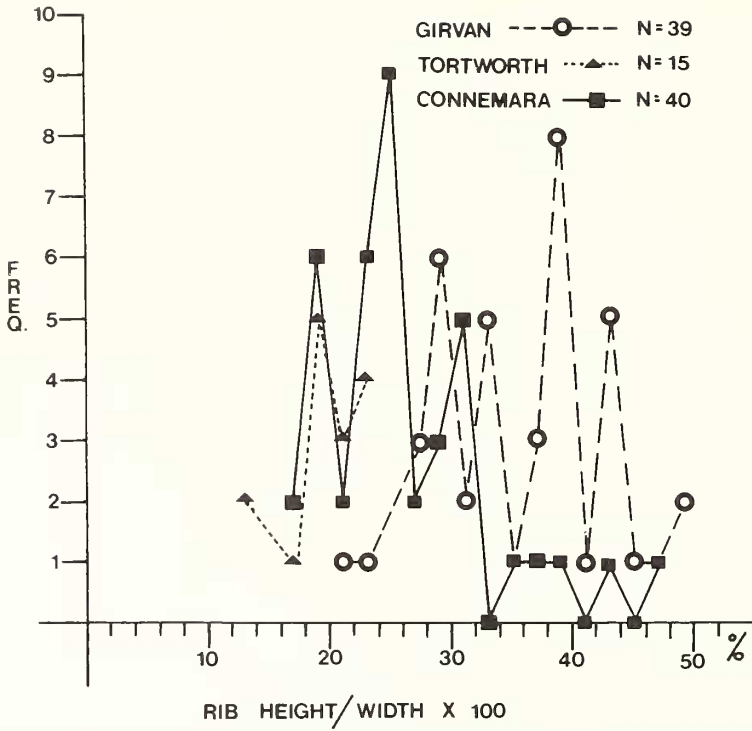


TEXT-FIG. 4. Frequency polygons of total rib numbers on valves of *E. curtisi* from Connemara, Tortworth and Girvan.

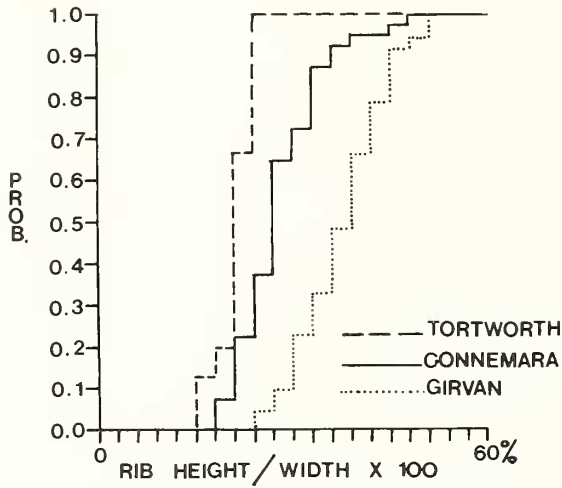


TEXT-FIG. 5. Comparison of the cumulative frequency polygons of the total rib numbers on valves of *E. curtisi* from Connemara, Tortworth and Girvan.

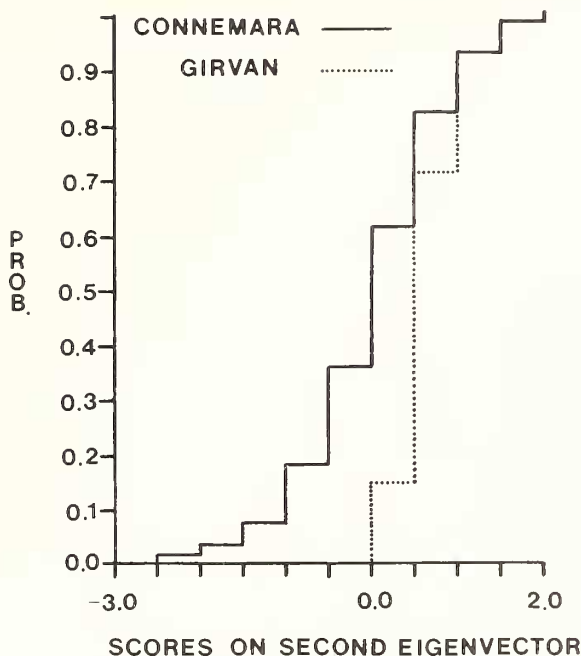
plot between the Irish and Scottish samples on the frequency polygon (Text-fig. 4) and significant differences were detected using the Kolmogorov-Smirnov test (at 1% level) between it and the material from Connemara ($D = 0.718$) and Girvan ($D = 0.620$). Although Ziegler (1966, p. 530) considered the modal rib density did not appear to behave consistently with time, despite the small samples in many collections, there is in fact a decrease in the number of ribs with time along this part of the lineage: a trend true, in general terms, for the lineage as a whole. Moreover, Ziegler's claim that the stratigraphically older *E. hemisphaerica* (reported modes of 14 and 16) has fewer ribs than *E. intermedia* (reported modes of 16 and 18) is not supported by the data in his table 3. Larger samples and counts of discrete rather than grouped rib numbers may help tighten this putative



TEXT-FIG. 6. Frequency polygons of rib-strength indices for brachial valves of *E. curtisi* from Girvan, Tortworth and Connemara.



TEXT-FIG. 7. Cumulative frequency polygons of rib-strength indices for brachial valves of *E. curtisi* from Girvan, Tortworth and Connemara.



TEXT-FIG. 8. Comparison of the scores on the second eigenvector (direction cosines: -0.278 , -0.423 , 0.862) for a PCA of variates sl, mw and pw for brachial valve exteriors of the Irish and Scottish *Eocoelia*. The Connemara specimens, *E. c. curtisi* have significantly smaller scores on this eigenvector ($D > 0.23$ at 1% level - Kolmogorov-Smirnov test).

trend. Sheldon (1987) has shown that evolutionary reversals are possible in otherwise unidirectional evolutionary trends, so it is conceivable that the overall trend of loss of ribs in the *Eocoelia* lineage may be influenced by periods of no loss or possible rib gain.

The rib strength of the taxa from Connemara, Girvan and Tortworth also displayed significant contrasts (Text-figs 6 and 7). Clearly, in view of the probability of some abrasion of the ribs during postmortem transport and modification with compaction, diagenesis and subsequent dissolution, this feature must be treated with some caution. Nevertheless, the clear decrease in rib strength with time is confirmed within the area of the lineage investigated here. Data from the Tortworth (Ziegler 1966, table 6), Connemara and Girvan specimens were compared statistically by F and t tests and the rib strengths of all three samples were compared with those of the stratigraphically older *E. intermedia*. But although the direction of the trend is confirmed, the timing of events within the trend would appear to be slightly retarded. The Irish *Eocoelia* ribs are significantly stronger than those of the nominate subspecies from Tortworth, having rib strengths similar to those of *E. intermedia* from Norbury, whereas the Girvan specimens have rib strengths similar to those of the stratigraphically younger *E. intermedia* from May Hill.

Many of the significant differences may be artefacts of sample comparisons of discrete and spatially isolated segments of a gradualist lineage. Further interpolation within the lineage will clearly strain the existing Linnean framework established for *Eocoelia* and will require a complete revision of its taxonomy or the recognition of categories of lesser rank than the subspecies (see also Sheldon 1987).

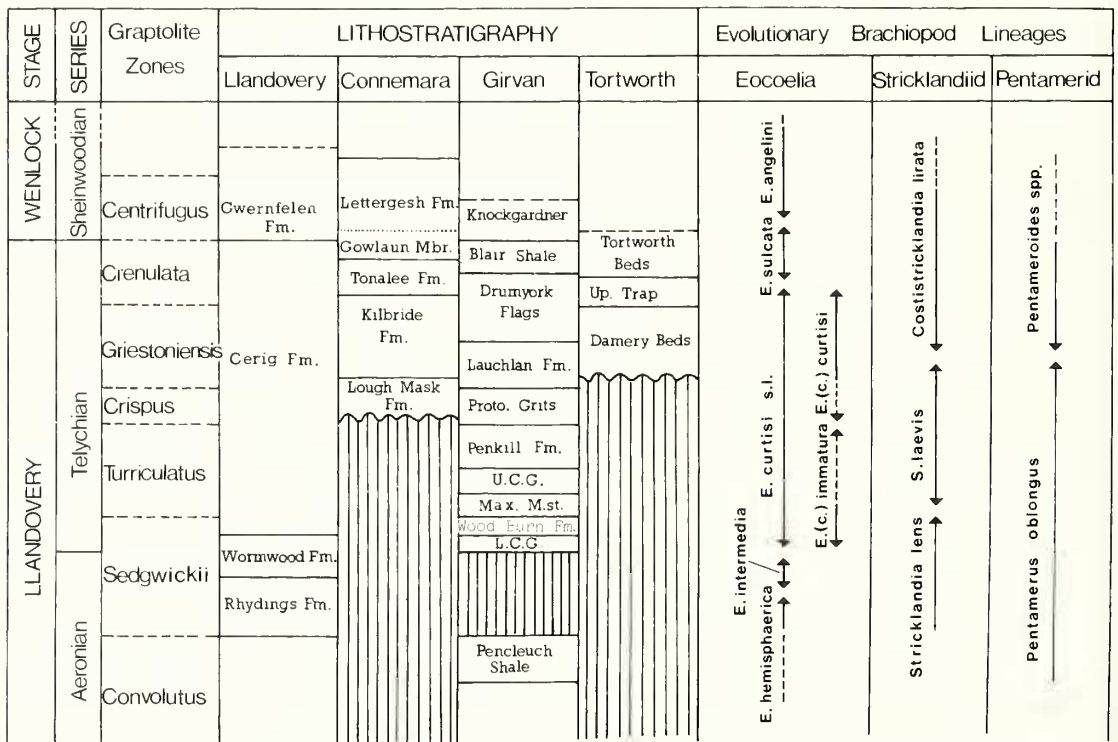
REFINEMENT OF THE *EOCOELIA* LINEAGE

The *Eocoelia* lineage, first established in detail by Ziegler (1966) and later modified by Cocks (1971), has more recently been summarized by Bassett (1984) in its entirety. Cocks *et al.* (1984) have, in revising the type Llandovery Series, documented the lower part of the lineage, summarized on Text-figure 9.

Ziegler (1966) identified a number of clear morphological trends during the phylogeny of *Eocoelia*: (i) strengthening of the articulating mechanisms with a trend towards deeper fossettes, stronger hinge plates and more robust teeth; (ii) reduction in the development of lips and deflections; and (iii) decline in rib strength.

All three samples investigated have well-developed crural fossettes, strong hinge plates and robust teeth, but umbonal chambers are lacking. Although these features are difficult to compare quantitatively, the samples from Girvan, Tortworth and the West of Ireland are consistent with those of *E. curtisi* Ziegler, 1966, confirming their inclusion in that species.

Fourteen percent ($N = 180$) of pedicle and brachial valves from the West of Ireland possessed a deflection whereas only 0.01% ($N = 220$) of pedicle and brachial valves from Girvan possessed the same feature. Clearly this interpolated trend is contrary to that seen in the lineage as a whole where there is an increase in the development of the deflection and lip. Although Ziegler (1966), in establishing a trend in this aspect of the *Eocoelia* shell, implied that the development of such features is not related to the size of the individual, deflections are in fact most commonly recorded from larger specimens. In the samples investigated by Ziegler (1966), the stratigraphically older species are



TEXT-FIG. 9. Lithostratigraphy of the Connemara, Girvan and Tortworth successions together with brachiopod lineages of correlative value displayed relative to the current graptolite biostratigraphy and chronostratigraphy for relevant parts of the lower Silurian. Abbreviations: L.C.G., Lower Camregan Grits; Max. M.st., Maxwellston Mudstones; U.C.G., Upper Camregan Grits; Proto., Protovirgularia, Up., Upper.

generally larger than those occurring high in the lineage. Ziegler (1966, table 7) reported a total absence of deflections on the shells of *E. curtisi*. The Irish samples are however larger (mean widths of 11.0 and 11.4 mm for dorsal and ventral exteriors, respectively) than the largest mean width (6.68 mm) reported in Ziegler (1966, table 5).

Within the *Eocoelia* lineage (Ziegler 1966) the transition between *E. intermedia* and *E. curtisi* is taken to occur in the lowest part of the *turriculatus* Biozone at a level correlated with the Aeronian/Telychian junction (Cocks *et al.* 1984). Therefore implicit in the definition of this boundary is the coincidence of the base of the *turriculatus* Biozone with the base of the Telychian. In the type area of the Llandovery Series diagnostic graptolite and shelly fossils are rare or absent at and adjacent to the Aeronian/Telychian stratotype boundary. Graptolites are, in fact, absent within the basal part of the Telychian in the type area, although faunas considered diagnostic of the lower half of the *turriculatus* Biozone (Cocks *et al.* 1984, p. 168) are reported 10 km from the stratotype section (Temple 1988, p. 879).

Ascending the type section, *E. curtisi* is first encountered in the lower part of the Cerig Formation, 35 m above the basal Telychian stratotype (Cocks *et al.* 1984, fig. 67), although it is assumed to occur throughout the lower part of the formation (Cocks *et al.* 1984, fig. 69), and thus within the lower part of the *turriculatus* Biozone. Cocks *et al.* (1984, p. 168) considered that the distribution of the relevant *Eocoelia* species and graptolites in the Penwhapple Burn section, near Girvan (Cocks and Toghill 1973) confirmed the coincidence of the base of the Telychian with the base of the *turriculatus* Biozone. However, at Girvan specimens hitherto assigned to *E. curtisi* (see Cocks and Toghill 1973) and assigned here to *E. curtisi immatura* subsp. nov. occur with *Pentamerus oblongus* in the Lower Camregan Grits. Although Cocks and Toghill (1973) do not record an *in situ* graptolite fauna from the overlying Wood Burn Formation, some slabs in the Gray Collection (British Museum of Natural History) from the Penkill locality suggest a correlation with the upper *sedgwickii* Biozone (Cocks and Toghill 1973, p. 226). The succeeding Maxwellston Mudstones contain a lower *turriculatus* Biozone fauna (Cocks and Toghill 1973, p. 227). Thus, rather than suggesting *E. curtisi* occurs with *turriculatus* Biozone graptolites, the Girvan section indicates a co-occurrence with graptolites of the *sedgwickii* Biozone.

Clearly, the lack of graptolite control across the Aeronian/Telychian boundary stratotype invites correlation of the upper part of the Wormwood Formation with either the lower *turriculatus* or upper *sedgwickii* biozones. However, in the absence of more equivocal faunal control in the type area, the faunal data from Girvan suggest the base of the Telychian may be better correlated with a horizon within the upper part of the notional *sedgwickii* Biozone. Moreover there is a gap of some 65 m in the *Eocoelia* lineage between the last occurrence of *E. intermedia* in the upper part of the Wormwood Formation and the first occurrence of *E. curtisi* in the Cerig Formation. If the lineage is as cosmopolitan as previous and current documentation suggests, then forms similar to *E. c. immatura*, together with graptolites of the *sedgwickii* Biozone, might be expected within this faunal hiatus.

North of the Girvan valley, in the Craighead inlier Cocks and Toghill (1973) have documented the co-occurrence of *E. curtisi* (*E. c. immatura* herein) and *Pentamerus oblongus* within the Lower Camregan Grits. Extension of the pit in Craighfin Wood (Cocks and Toghill 1973, p. 217) has yielded a new fauna in higher strata: a species of *Pentameroides* occurs with a number of poorly preserved specimens assigned, on the basis of their outlines and rib numbers, to *E. cf. curtisi curtisi*. Poor exposure and complex faulting in this part of the inlier presents considerable stratigraphical difficulties; nevertheless, the co-occurrence of *Pentameroides* and a form approximating to the nominate subspecies of *E. curtisi* supports the correlations presented in Text-figure 9.

In the west of Ireland, *E. curtisi curtisi* occurs with *Costistricklandia lirata* and *Pentameroides* within the Kilbride Formation, presumably near the top of its range. Although no diagnostic fossils are present in the overlying Tonalee Formation (Doyle *et al.* 1990) the succeeding Benbeg Mudstones contain *crenulata* Biozone graptolites (Rickards 1973).

SYSTEMATIC PALAEONTOLOGY

Family TRIGONIRHYNCHIIDAE McLaren, 1965

Genus EOCOELIA Nikiforova, 1961 (*in* Nikiforova and Andreeva 1961)

Remarks. Cocks (1978, p. 149) transferred *Eocoelia* from its traditional site within the Atrypida, on the basis of an undescribed species of *Eocoelia*, from the Idwian (Aeronian) of Shropshire, with similarities to *Rostricellula*.

Eocoelia curtisi curtisi Ziegler, 1966

Text-fig. 10

1867 *Atrypa? hemisphaerica* J. de C. Sowerby; Davidson, p. 136 (*pars*), pl. 13, figs 24–30*a*, non fig. 23.

1966 *Eocoelia curtisi* Ziegler, p. 537 (*pars*), pl. 83, figs 7 and 8; pl. 84, figs 12–17.

Holotype. OUM C3241; an internal mould of a pedicle valve from the Damery Beds (Telychian) of the Tortworth Inlier, Gloucestershire; pl. 84, figs 15, 16, 17 of Ziegler 1966.

Material. About 200 pedicle valves and 200 brachial valves, all virtually complete, none conjoined.

Diagnosis. Nominate subspecies of *E. curtisi* with 7–16 (mode 11 – Connemara or 12 – Tortworth) strong ribs developed on brachial valve exteriors; maximum width posterior to midvalve length and rib strengths about one-quarter.

Description

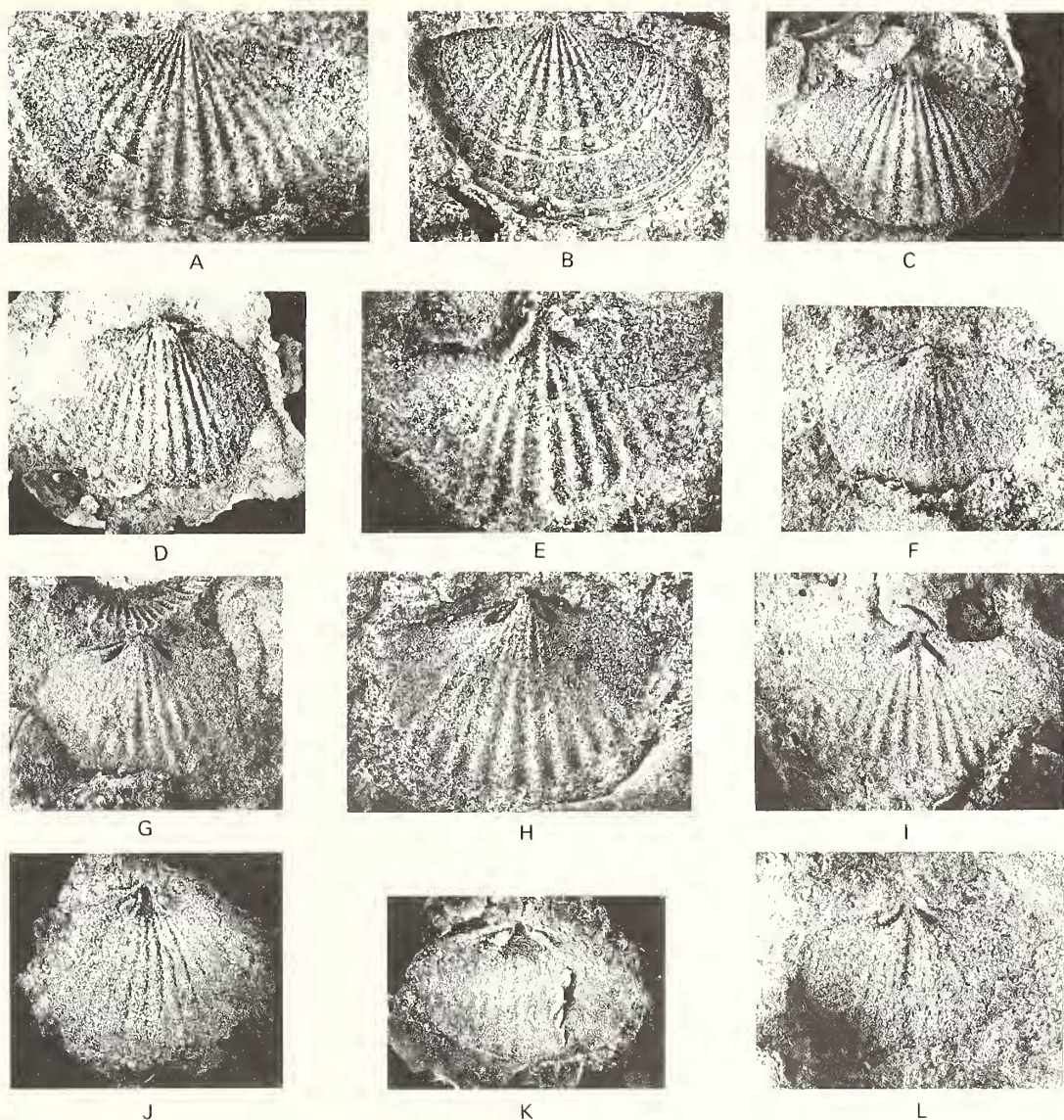
Exterior. Medium-sized, planoconvex valves of transversely subquadrate to subelliptical outline with maximum width posterior to mid-valve length. Hinge line about four-fifths maximum width, cardinal extremities obtuse and rounded. Pedicle valve about three-quarters as long as wide and about one-quarter as deep as long; anterior and lateral profiles convex medianly but in later growth stages growth vectors change to produce anterolateral flattening. Maximum depth occurs between one-fifth and two-fifths valve length. Brachial valve about three-quarters as long as wide, essentially flat with faint median sulcus and flatly convex flanks. Deflection of valve profile present on 14% of pedicle and brachial valves ($N = 180$). Ornament of strong costae of evenly rounded, semicircular profile, numbering 7–15 on 1, 3, 2, 20, 34, 29, 12, 7, 2 valves and with mean (variance) rib strength (height/width * 100) of 26.4 (43.5) for 40 brachial valves; costae subdued or absent posterolaterally. Concentric growth lines absent posteriorly but accentuated anteriorly.

Ventral interior. Delthyrial chamber moderately deep with faint pedicle callist rarely developed in posterior half. Large cyrtomatodont teeth, oval to triangular in dorsal view with rounded anterior surfaces. Dental plates absent; teeth attached directly to shell wall. Large fossettes cut deeply into medial face of teeth extending into shell wall. Muscle scars not impressed.

Dorsal interior. Socket plates large, well developed, almost rectangular in ventral view, diverging at 55–75 degrees and supported posteriorly on broad, raised notothyrial platform; cardinal process very rarely (< 1%) present. Sockets deep, conical and widely divergent. Median ridge arising anterior to notothyrial platform and extending to about one-half valve length. Muscle scars feebly impressed.

*Measurements and statistics**Brachial valve exteriors*

Variates	sl	mw	pm
Sample size	110	111	110
Means	7.71	11.0	2.46
Variance-covariance matrix	2.29	2.87	0.58
		4.92	0.74
			0.39



TEXT-FIG. 10. *Eocoelia curtisi curtisi* Ziegler, from the lower part of the Kilbride Formation, north Connemara. A, external mould of brachial valve, JMM Br1000, $\times 3$. B, external mould of brachial valve, JMM Br1001, $\times 3$. C, latex cast of pedicle valve exterior, JMM Br1002, $\times 2$. D, latex cast of pedicle valve exterior, JMM Br1003, $\times 3$. E, latex cast of brachial valve interior, JMM Br1004, $\times 3$. F, internal mould of pedicle valve, JMM Br1005, $\times 2$. G, internal mould of pedicle valve, JMM Br1006, $\times 2$. H, internal mould of pedicle valve, JMM Br1007, $\times 3$. I, internal mould of brachial valve, JMM Br1008, $\times 3$. J, latex cast of pedicle valve interior, JMM Br1009, $\times 3$. K, latex cast of pedicle valve interior, JMM Br1010, $\times 3$. L, internal mould of brachial valve, JMM Br1011, $\times 3$.

Brachial valve interiors

Variates	sl	mw	mb	bl	ln
Sample size	104	105	111	111	111
Means	8.00	10.8	1.90	1.24	0.82
Variance-covariance matrix	1.76	2.47	0.43	0.23	0.13
		4.98	0.81	0.40	0.19
			0.20	0.09	0.04
				0.08	0.04
					0.03

Pedicle valve exteriors

Variates	sl	mw	pm	pt
Sample size	98	100	100	100
Means	8.06	11.4	2.82	2.80
Variance-covariance matrix	2.06	2.17	0.61	0.57
		3.95	0.66	0.53
			0.32	0.23
				0.36

Pedicle valve interiors

Variates	sl	mw	lc	mc	sc	mt
Sample size	96	96	96	96	96	96
Means	8.21	11.2	1.23	2.01	1.09	2.42
Variance-covariance matrix	2.07	2.37	0.18	0.35	0.21	0.44
		4.02	0.25	0.54	0.26	0.65
			0.06	0.06	0.04	0.07
				0.15	0.06	0.16
					0.05	0.07
						0.21

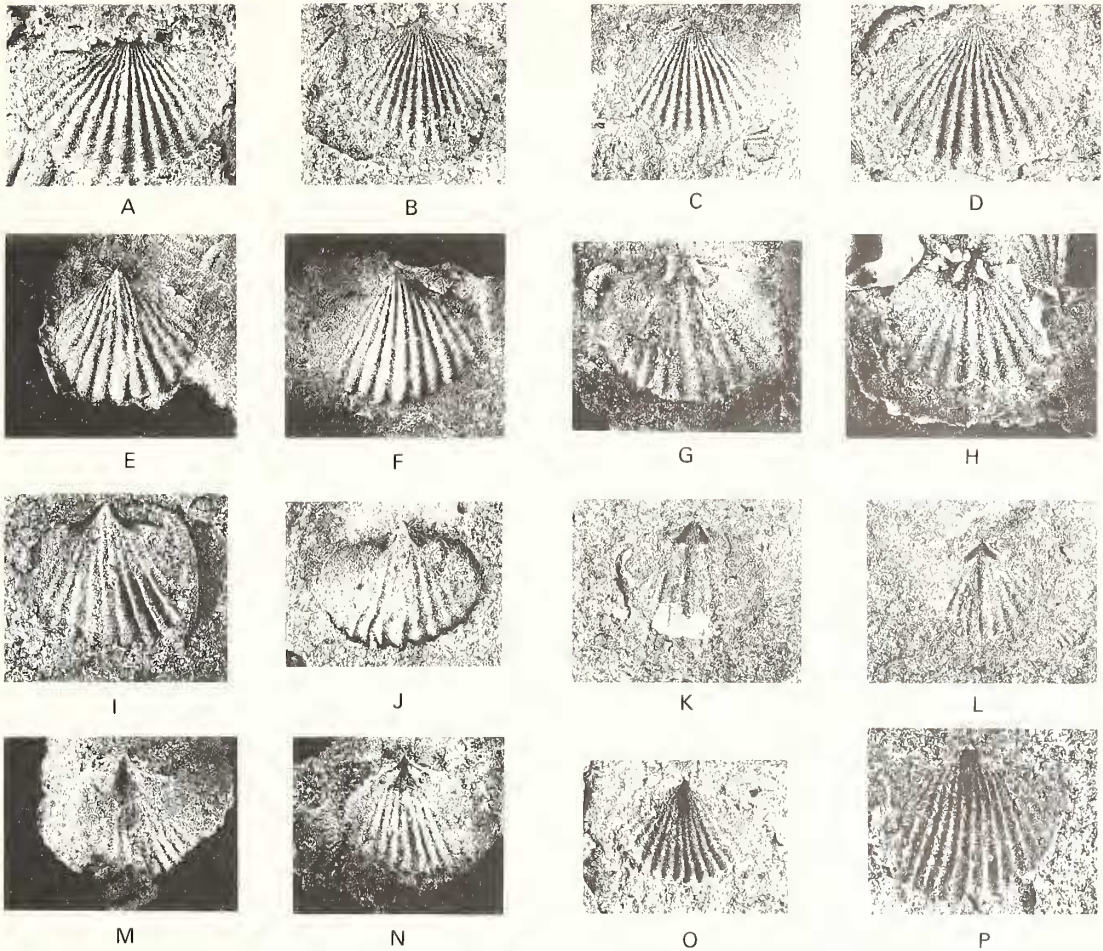
Remarks. The description of *E. curtisi curtisi*, presented here, is based exclusively on material from the lower part of the Kilbride Formation, which crops out along the northern margin of Connemara. The Irish specimens are considered morphologically identical to the type and topotype material of the nominate subspecies from Tortworth except for the development of the ribs. The ribbing strengths of the various *E. curtisi* morphs have been discussed above. However, analysis of the rib counts of the Tortworth and Connemara specimens presents taxonomic difficulties. A Kolmogorov-Smirnov test, as noted above, indicates a significant difference between the two frequency distributions. The Irish material has a modal value of 11 ribs, that from Tortworth has a mode of 12. However, the sample from Tortworth is disproportionately smaller than that from Ireland. Moreover it is probable that the Connemara specimens are from slightly younger horizons than those from Tortworth, thus confirming the trend of decreasing rib number with decreasing time. Since the Irish *E. curtisi* agrees in all other aspects with the nominate subspecies it is not separated on the basis only of the modal rib counts. However, it may be suggested the two represent chronological morphs of the same subspecies which a more rigorous investigation of more material may confirm or reject.

Eocoelia curtisi Ziegler, 1966 *immatura* subsp. nov.

Text-fig. 11

- 1867 *Atrypa? hemisphaerica* J. de C. Sowerby; Davidson, p. 136 (pars), pl. 13, figs 25, 27-30.
 1973 *Eocoelia curtisi* Ziegler; Cocks and Toghil, p. 225, pl. 3, figs 1-3.

Name. Latin *immatura*, youthful morphological characteristics.



TEXT-FIG. 11. *Eocoelia curtisi* Ziegler *immatura* subsp. nov. from the Lower Camregan Grits, Penwhapple Burn, Girvan. A, external mould of brachial valve, JMM Br1012, $\times 3$. B, external mould of brachial valve, JMM Br1013, $\times 2$. C, external mould of brachial valve, JMM Br1014, $\times 2$. D, external mould of brachial valve, JMM Br1015, $\times 3$. E, latex cast of pedicle valve exterior, JMM Br1016, $\times 2$. F, latex cast of pedicle valve exterior, JMM Br1017, $\times 3$. G, latex cast of brachial valve interior, JMM Br1018, $\times 3$. H, latex cast of brachial valve interior, JMM Br1019, $\times 2$. I, internal mould of pedicle valve, JMM Br1020, $\times 2$. J, internal mould of pedicle valve, JMM Br1021, $\times 2$. K, internal mould of brachial valve, JMM Br1022, $\times 2$. L, internal mould of brachial valve, JMM Br1023, $\times 2$. M, latex cast of pedicle valve interior, JMM Br1024, $\times 2$. N, latex cast of pedicle valve interior, JMM Br1025, $\times 2$. O, External mould of pedicle valve, JMM Br1026, $\times 2$. P, external mould of pedicle valve, JMM Br1027, $\times 3$. All type and figured specimens are deposited in the James Mitchell Museum, University College Galway, Ireland.

Holotype. JMM Br1020; an internal mould of a pedicle valve from the Lower Camregan Grits, Penwhapple Burn, Girvan, SW Scotland.

Material. About 150 pedicle valves and about 180 brachial valves, all virtually complete, none conjoined.

Diagnosis. Small subspecies of *E. curtisi* with 13–19 (mode 15) strong ribs developed on brachial valve exteriors; maximum width at or near midvalve length and rib strength of about one-third.

Description

Exterior. Small, planoconvex valves of subquadrate outline with maximum width at or near mid-valve length. Hinge line about three-quarters maximum width with obtusely rounded cardinal extremities. Pedicle valve about four-fifths as long as wide and about one-quarter as deep as long with maximum depth at about one-third valve length. Delthyrium relatively wide and open. Brachial valve about four-fifths as long as wide and essentially flat. Ventral and dorsal interareas obsolete. Ornament of relatively strong ribs of evenly rounded profile developed over entire valve surface and numbering 13–19 on 11, 34, 40, 13, 4, 0, 1 valves with rib strength of mean (variance) 35.8 (47.4) for 38 brachial valves.

Ventral interior. Relatively deep delthyrial chamber flanked by large cyrtomatodont teeth, oval in dorsal view with rounded anterior surfaces; dental plates absent. Dental fossettes cut deeply into medial face of teeth. Muscle scars not impressed.

Dorsal interior. Large, robust socket plates, elongately rectangular in ventral view and distal parts anteriorly divergent on low notothyrial platform. Deep, divergent conical sockets. Broad median ridge extending anteriorly from margin of notothyrial platform. Muscle scars not impressed.

*Measurements and statistics**Brachial valve exteriors*

Variates	sl	mw	pm
Sample size	103	103	103
Means	5.61	6.90	2.30
Variance-covariance matrix	0.73	0.80	0.24
		1.14	0.32
			0.14

Brachial valve interiors

Variates	sl	mw	mb	nl	ln
Sample size	79	79	79	79	79
Means	5.84	7.08	1.44	1.14	0.54
Variance-covariance matrix	0.82	1.00	0.12	0.10	0.05
		1.49	0.19	0.15	0.08
			0.08	0.04	0.01
				0.04	0.01
					0.01

Pedicle valve exteriors

Variates	sl	mw	pm	pd	pt
Sample size	117	117	117	117	117
Means	5.35	6.47	2.34	1.62	13.2
Variance-covariance matrix	2.19	1.94	0.72	0.52	0.39
		2.86	0.91	0.69	0.66
			0.43	0.27	0.18
				0.28	0.10
					1.53

Pedicle valve interiors

Variates	sl	mw	lc	mc	sc	mt
Sample size	44	44	44	44	44	44
Means	5.99	6.80	0.66	1.33	0.55	1.55

Variance-covariance matrix	0.89	0.71	0.13	0.12	0.09	0.14
		0.61	0.10	0.11	0.07	0.13
			0.03	0.02	0.02	0.02
				0.03	0.01	0.03
					0.02	0.01
						0.04

Remarks. The Scottish material, hitherto referred to *E. curtisi* by Cocks and Toghil (1973), differs in two main respects from the nominate subspecies. First the maximum width is at or near the mid-valve length and secondly it has more and stronger ribs. Taken together, the morphological contrasts may be interpreted as specific differences; however, the Girvan, Connemara and Tortworth samples are characterized by well-developed crural fossettes, strong hinge plates and robust teeth; umbonal chambers are absent. This association of characteristics conventionally describes *E. curtisi*; the differences, therefore, are accorded only subspecific status.

Acknowledgements. We thank A. Davis for assistance, P. Powell for access to material in the Oxford University Museum and W. S. McKerrow for many wide-ranging discussions. Doyle and Höey were financed by Postgraduate Fellowships at University College Galway and Harper is grateful to the Royal Irish Academy for help with field expenses.

REFERENCES

- BASSETT, M. G. 1984. Lower Palaeozoic Wales – a review of studies in the past 25 years. *Proceedings of the Geologists' Association*, **95**, 291–311.
- COCKS, L. R. M. 1971. Facies relationships in the European Lower Silurian. *Mémoires du Bureau de Recherches Géologiques et Minières*, **73**, 223–227.
- 1978. A review of British Lower Palaeozoic brachiopods, including a synoptic revision of Davidson's monograph. *Monograph of the Palaeontographical Society*, **131** (549), 1–256.
- and TOGHILL, P. 1973. The biostratigraphy of the Silurian rocks of the Girvan district, Scotland. *Journal of the Geological Society of London*, **129**, 209–243, pls 1–3.
- WOODCOCK, N. H., RICKARDS, R. B., TEMPLE, J. T. and LANE, P. D. 1984. The Llandovery Series of the type area. *Bulletin of the British Museum (Natural History)*, (Geology), **38**, 131–182.
- DAVIDSON, T. 1867. A monograph of the British fossil Brachiopoda. Part VII. No. II. The Silurian Brachiopoda. *Monograph of the Palaeontographical Society*, **3**, 89–168, pls 13–22.
- DOYLE, E. N. 1989. The biostratigraphy and sedimentology of the Lower Silurian (Llandovery) rocks of north Galway. Unpublished Ph.D. thesis, National University of Ireland.
- HARPER, D. A. T. and PARKES, M. A. 1990. The Tonalee fauna: a deep-water shelly assemblage from the Llandovery rocks of the West of Ireland. *Irish Journal of Earth Sciences*, **11**, 127–143.
- HARPER, D. A. T. and RYAN, P. D. 1987. PALSTAT – a statistical package for palaeontologists. Palaeontological Association and Lochce Publications, Dundee, Scotland.
- LAIRD, M. G. and MCKERROW, W. S. 1970. The Wenlock sediments of northwest Galway, Ireland. *Geological Magazine*, **107**, 297–317.
- MCLAREN, D. J. 1965. Family Trigonirhynchidae McLaren, n. fam. H559–H562. In MOORE, R. C. (ed.), *Treatise on invertebrate paleontology. Part H. Brachiopoda*. Geological Society of America and Kansas University Press, Boulder, Colorado and Lawrence, Kansas, 927 pp.
- NIKIFOROVA, O. I. and ANDREEVA, O. N. 1961. Stratigraphy of the Ordovician and Silurian of the Siberian Platform and its palaeontological basis (Brachiopods). *Biostratigraphiya Paleozoya Sibirskov Platformy, Leningrad*, **1**, 1–412, pls 1–56.
- PIPER, D. J. W. 1972. Sedimentary environments and palaeogeography of the late Llandovery and earliest Wenlock of north Connemara. *Quarterly Journal of the Geological Society of London*, **128**, 33–51.
- RICKARDS, R. B. 1973. On some highest Llandovery red beds and graptolite assemblages in Britain and Eire. *Geological Magazine*, **110**, 70–72.
- SHELDON, P. R. 1987. Parallel gradualistic evolution of Ordovician trilobites. *Nature*, **330**, 561–563.
- TEMPLE, J. T. 1988. Biostratigraphical correlation and the stages of the Llandovery. *Journal of the Geological Society of London*, **145**, 875–879.

- ZIEGLER, A. M. 1965. Silurian marine communities and their environmental significance. *Nature*, **207**, 270–272.
— 1966. The Silurian brachiopod *Eocoelia hemisphaerica* (J. de C. Sowerby) and related species. *Palaeontology*, **9**, 523–543, pls 83 and 84.

E. N. DOYLE¹, A. N. HÖEY² and D. A. T. HARPER

Department of Geology
University College
Galway, Ireland

Present addresses:

¹Department of Geology
University of the West Indies
Mona, Kingston 7, Jamaica

²Department of Geology
University College
Belfield, Dublin, Ireland

Typescript received 2 January 1990
Revised typescript received 7 March 1990